ANATOMY, PATTERNS OF OCCURRENCE, AND NATURE OF THE CONULARIID SCHOTT

by HEYO VAN ITEN

Abstract. Conulariid specimens that terminate adapically in a transverse wall, or schott, have been interpreted in several ways. These interpretations have been based more on analogy with extant organisms than on evaluation of fossil material. Currently favoured interpretations are that (1) schott-bearing specimens represent individuals that were severed, in life, by currents; (2) schott-bearing specimens were free-swimming individuals; (3) schott-bearing specimens represent non-injured, sessile individuals that retracted the apical part of their soft body toward the oral end, as part of their normal life history. Examination of the test cavity of conulariid specimens that do not terminate in a schott, and analysis of the frequency of occurrence of schott-bearing specimens in low- versus high-energy sedimentary deposits, indicate that the most likely interpretation of schott-bearing specimens is that they represent living individuals severed by currents. Proponents of a scyphozoan affinity for conulariids have generally interpreted schott-bearing specimens as conulariid medusae, one of the alternatives not favoured by the present analysis. In spite of this, the interpretation of schott-bearing specimens as severed individuals is consistent with the hypothesis that conulariids and scyphozoans were closely related.

Previous discussions of the mode of life and life history of conulariids have presented compelling evidence that conulariid specimens terminating in a narrow apex (Text-fig. 1A) were sessile animals, either free-standing and attached at the apex to shell material or other substrates, or embedded in massive sponges or bryozoans (e.g. Sinclair 1948; Finks 1955, 1960; Rooke and Carew 1983; Babcock *et al.* 1987; Harland and Pickerill 1987; Van Iten 1991*a*). Yet disagreement persists as to the nature of conulariid specimens whose apical end, now truncated some distance above the apex, terminates in a more or less smooth, generally convex transverse wall (Text-fig. 1B). This structure, referred to by Kiderlen (1937) as the schott (the German word for bulkhead), was originally interpreted as one of a series of internal septae, homologous to the septae of nautiloid cephalopods (Hall 1847). Although schott-bearing specimens have been found that exhibit one or two additional schotts above the terminal one (Babcock and Feldmann 1986*a*; see also below), it is now agreed that the conulariid schott and nautiloid septa are not homologous structures (e.g. Werner 1966, 1967; Bischoff 1978; Grasshoff 1984; Babcock and Feldmann 1986*a*).

More recent discussions of the nature of the conulariid schott have focused on one or more of the following three alternatives: (1) the schott was a cicatrix, produced in response to severance of the body by currents (Werner 1966, 1967); (2) the schott was an autotomy scar, produced when the adult conulariid detached from its apical end and assumed a free-swimming mode of life (e.g. Kiderlen 1937; Bouček 1939; Termier and Termier 1949, 1953; Moore and Harrington 1956; Chapman 1966; Kozłowski 1968; Bischoff 1978; Grasshoff 1984); (3) the schott was a regular growth feature, produced upon attainment of a certain age (Sinclair 1948; Babcock and Feldmann 1986*a*). With the exceptions of Termier and Termier (1949, 1953) and Kozlowski (1968), advocates of the hypothesis that the conulariid schott was produced in response to assumption of a free-swimming mode of life interpret schott-bearing conulariids as similar to medusae of scyphozoan cnidarians, a group that has been widely regarded as the most likely candidate for an extant nearest relative of conulariids (e.g. Kiderlen 1937; Bouček 1939; Moore and Harrington 1956; Chapman 1966; Werner 1966, 1967; Bischoff 1978; Grasshoff 1984; Van Iten 1991*b*). Their interpretation of

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A B

TEXT-FIG. 1. A, *Archaeoconularia granulata* (Hall); AMNH 791; Middle Ordovician (Trenton Group); New York, USA; two specimens, both broken just above the apex and with their apical end (arrows) situated immediately adjacent to a straight-shelled nautiloid (probably *Endoceras proteiforme* Hall), × 0·88. B, ?*Conularia* sp.; UMMP 259; Upper Devonian (English River Siltstone); southeast Iowa, USA; crumpled specimen terminating in a prominent, outwardly convex schott, × 1.

the conulariid schott, here designated the alternation of generations hypothesis, is based on analogy with scyphozoans exhibiting alternating polypoid and medusoid life stages.

Werner (1966, 1967), himself a proponent of a scyphozoan affinity for conulariids, proposed that schott-bearing specimens represent polypoid individuals that were severed by currents, in life, and survived to heal their damaged apical end as they lay on their side. His interpretation, here designated the severance by currents hypothesis, is based on the observation that conulariid tests are often extremely thin (with tests 30 or more cm long but commonly less than 0·01 cm thick; Van Iten in prep.), and on analogy with coronatid scyphozoan polyps whose theca and soft parts have been severed experimentally. As documented by Werner (1966, 1967) and Chapman and Werner (1972), coronatid polyps that survive severance cover exposed soft tissues by producing a thin, smooth sheet of periderm that is similar in microstructure and gross morphology to the conulariid schott.

The third alternative, offered with essentially no support, suggests that when conulariids reached a certain age, they retracted the apical part of their soft body toward the aperture, producing a schott to seal off the portion of the test cavity just abandoned. This interpretation will be referred to here as the apical retraction hypothesis. (A similar hypothesis, proposed by Babcock and Feldman (1984, p. 17), is that conulariids were pseudoplanktonic organisms and that 'at certain points in their life cycle, sections of the periderm at the apex divided along the last-formed transverse wall [schott] and fell to the ocean floor'.)

The present paper seeks to evaluate the foregoing interpretations of the conulariid schott through analysis of its occurrence within conulariids, and through analysis of patterns of occurrence of schott-bearing specimens with respect to sedimentary facies. A critical prediction of the hypothesis that the conulariid schott was a regular growth feature, produced upon attainment of a certain age (apical retraction hypothesis), is that specimens that preserve their apex (pointed specimens) and belong to taxa that have yielded schott-bearing specimens should exhibit one or more schotts within the test cavity (provided, of course, that such specimens were old enough to form schotts).

Two key predictions of the severance by currents hypothesis are that (1) specimens preserving the apex (and therefore not severed) should not exhibit internal schotts; and (2) percentages of schott-bearing specimens in samples of conulariids should vary significantly, depending on the sedimentology of the deposits hosting the samples. As noted by previous workers (e.g. Barrande 1867; Bouček 1928; Sinclair 1948; Moore *et al.* 1952; Havlíček and Vaněk 1966), conulariids occur in large numbers in a variety of marine strata. These include strata that were deposited under conditions of extremely low physical energy (e.g. dark, laminated, deep-shelf shales and lime mudstones), and strata deposited under conditions of relatively high physical energy (e.g. shallow-shelf quartz sandstones and lime grainstones). If schott formation was associated with severance by currents, then not only should schotts be absent in the test cavity of specimens that were not severed in life, but proportions of schott-bearing specimens should be significantly higher in samples from high-energy deposits than in samples from low-energy deposits (all other factors being equal).

This pattern of occurrence would not be expected were schott formation associated with assumption of a free-swimming mode of life (or, alternatively, if conulariids were pseudoplanktonic organisms that sometimes dropped to the sea floor). This is because schott formation would have been mediated principally by the life history of the developing organism, rather than by physical characteristics of the surrounding water, and because the chances of free-swimming (or pseudoplanktonic) conulariids being preserved in fine grained, low energy deposits, where conulariids commonly occur in great abundance (e.g. Sinclair 1948; Moore *et al.* 1952) and have been found preserved *in situ* (e.g. Rooke and Carew 1983), would have been at least as good as the chances of their being preserved in relatively coarse grained, higher energy deposits. In short, the alternation of generations hypothesis predicts that proportions of schott-bearing specimens in low- versus high-energy deposits should not be significantly different.

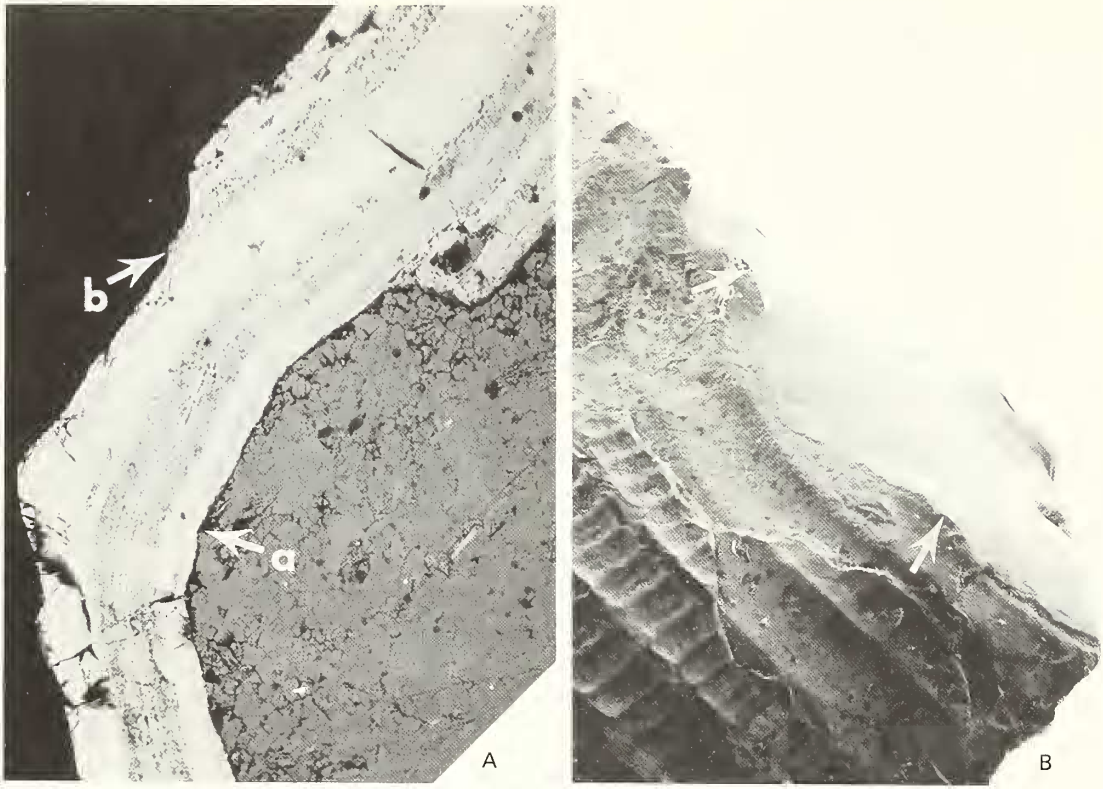
Details of the anatomy of the conulariid schott and schott-bearing conulariids are covered in a Ph.D. dissertation by Sinclair (1948), but this work has not been published. To rectify this deficiency in the conulariid literature, and to present additional information having a potential bearing on alternative interpretations of the cause(s) of schott formation, data on the anatomy of the conulariid schott will be presented in the following section.

Schott-bearing specimens are currently known from five of the twenty-one recognized conulariid genera, namely *Anaconularia* Sinclair, *Archaeoconularia* Bouček, *Conularia* Miller, *Metaconularia* Foerste, and *Paraconularia* Sinclair. The present study is based on direct examination of approximately 1100 specimens of these genera, supplemented by published data on approximately 500 additional specimens. Information on the location of specimens and explanations of repository abbreviations used in the remainder of this paper are presented in the appendices.

ANATOMY OF THE SCHOTT AND SCHOTT-BEARING CONULARIIDS

The conulariid schott is built of numerous, extremely thin (about 1 μm), apatitic lamellae, alternatively dense and vacuity-rich, that parallel its surface (Text-fig. 2A). It consists of a transverse portion, or wall, and a longitudinal portion, or sleeve, that extends along the inner surface of the faces proper, toward the aperture. Tracing of schott lamellae in sectioned specimens preserved near their aperture revealed that the sleeve probably extended all the way to the aperture. The wall/sleeve boundary tends to be irregular (Text-fig. 2B), and the surface defined by this boundary may be oriented more or less perpendicular to the test's long axis or inclined at a high angle to it. The wall may be adapically convex, more or less planar, or adaperturally convex. Its surface may be smooth or finely wrinkled, with wrinkles usually concentrated along the wall/sleeve boundary and oriented at various angles to it. In some cases, the wall exhibits a small dimple or dimple-bearing protuberance, usually situated at or near its centre.

As noted by previous investigators (e.g. Barrande 1867; Slater 1907), the distance between the schott and the former apex (estimated by extending the corners of the test to their point of intersection) varies between specimens. For example, in *Conularia trentonensis* Hall (Middle to Upper Ordovician, North America), characterized in life by a maximum test length of at least 10 cm



TEXT-FIG. 2. A, *Conularia trentonensis* Hall; UMMP 7000; Middle Ordovician (Trenton Group); New York, USA; scanning electron photomicrograph of part of a longitudinal section through a terminal schott, showing the finely laminate microstructure, the wall-sleeve junction (arrow labelled 'a'; the sleeve is the portion above the arrow), and the contact between the sleeve and the face proper (arrow labelled 'b') × 250. B, *C. trentonensis* Hall; UMMP 66012; Middle Ordovician (Trenton Group); New York, USA; oblique view of part of the external surface of a terminal schott with a relatively prominent, dimple-bearing protuberance; the wall-sleeve boundary (arrows) is irregular and associated with fine wrinkling of the wall, × 22.

(Van Iten in prep.), schotts occur at test widths ranging from about 1·5 to 6·0 mm (N = 29, mean = 3·6 mm, S.D. = 1·1 mm), or from about 10 to 40 mm above the apex.

The cross-sectional geometry of schott-bearing specimens may be more or less rectangular, or strongly rhombic, in some cases to such an extent that members of one pair of opposing corners nearly touch each other (Kiderlen 1937; Sinclair 1948). In specimens showing a strongly rhombic cross section, the schott itself is often smoothly curved and shows no evidence of compactional distortion. This suggests that rhombic specimens terminating in a non-compacted schott exhibited a rhombic cross-sectional geometry while alive (Sinclair 1948).

Although most schott-bearing specimens documented by previous workers (e.g. Barrande 1867; Bouček 1928; Kowalski 1935) exhibit only one schott, some investigators (e.g. Barrande 1867; Slater 1907) maintained that conulariids usually produced multiple schotts. This interpretation was based on the observation that the distance between the schott and the former apex varies between specimens (presumably reflecting post-mortem break-up of specimens), and on the discovery of specimens exhibiting more than one schott. However, present examination of the test cavity of 207 specimens terminating in a schott, including 49 specimens preserving test material (e.g. Text-fig. 1B) and 158 specimens preserved as sandstone steinkerns (Appendix 1), yielded only two specimens, USNM 373992 (*Conularia quichua* Ulrich) and AMNH 42316 (*C. trentonensis* Hall), having more than one schott (both of these specimens have two schotts, with the second, internal schott situated several millimetres above the terminal one). Previous authors (Steinmann and Döderlein 1890; Slater 1907; Kiderlen 1937; Sinclair 1948) have collectively reported six specimens bearing multiple schotts. Five of these specimens have two schotts, and one of them (Steinmann and Döderlein 1890) has three schotts. These six specimens constitute a very small fraction of the total number (estimated by the present author to be at least 500) of schott-bearing specimens reported by previous authors. Most of these specimens are preserved as sandstone steinkerns or show extensive exfoliation, thus revealing their test cavity. Neither these nor any of the specimens here examined (Appendix 1) exhibit a schott at their apertural end, where one might expect to find a schott (at least occasionally) had conulariids normally produced multiple schotts and undergone break-up. In short, it appears that conulariids almost always produced only one schott.

In specimens having multiple schotts, the sleeve of the schott situated closest to the aperture rests on the inner (adaxial) surface of the sleeve of its neighbour (Sinclair 1948). Together with the observation that schotts are lamellar, with sleeves that extended all the way to the aperture, this suggests that the sequence of formation of multiple schotts was adapertural in direction, and that schotts were produced by centripetal accretion of whole lamellae, along the entire length of the soft body.

OCCURRENCE OF SCHOTTS IN THE TEST CAVITY OF POINTED SPECIMENS

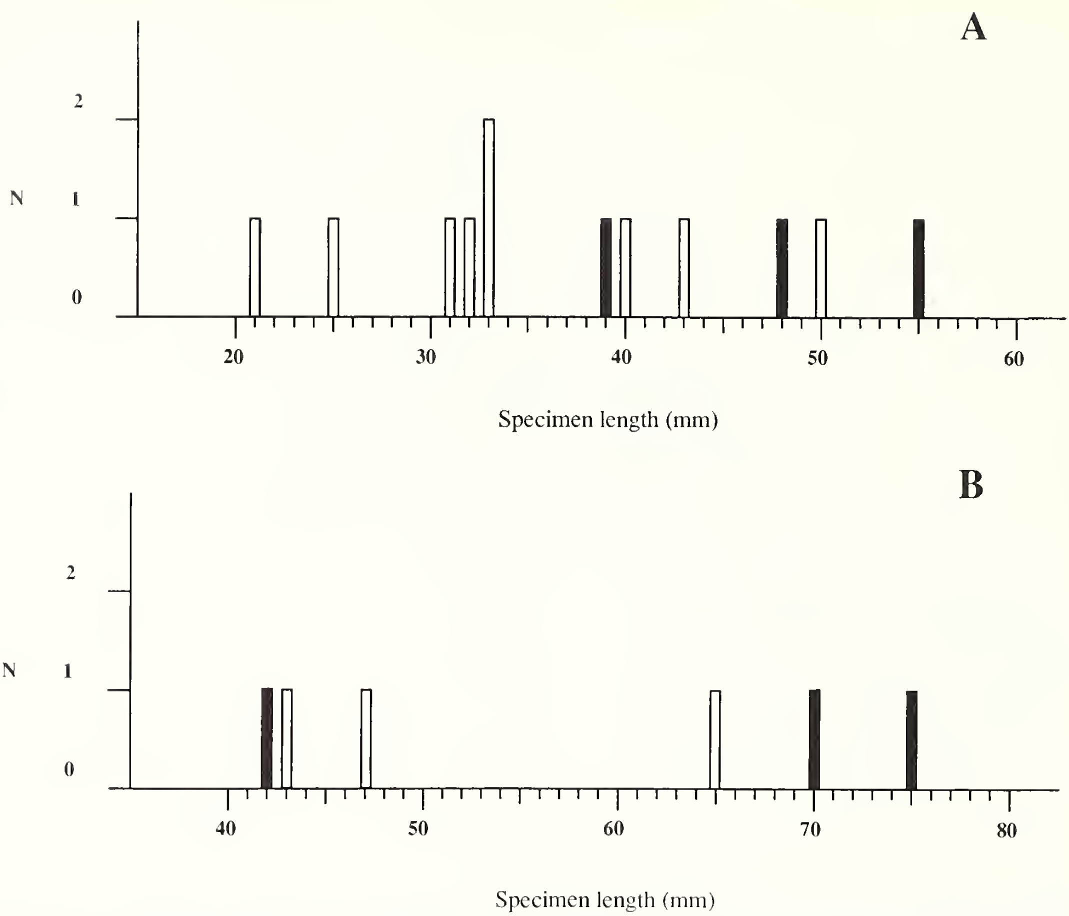
To determine if schotts occur in the test cavity of conulariid specimens that do not terminate in a schott (but that belong to species or genera that have yielded schott-bearing specimens), observations were made on specimens of *Archaeoconularia granulata* (Hall) (Text-fig. 1A; $N = 2$), *Metaconularia manni* (Roy) ($N = 12$), *Conularia splendida* Billings (N = 9), *C. trentonensis* Hall ($N = 115$), and several species of *Paraconularia* ($N = 15$) (Appendix 2). Except for certain *Paraconularia* (Appendix 2), all of the 153 specimens in this sample terminate at a test width of 1 mm or less, well below usual levels of occurrence of terminal schotts in conspecific or congeneric, schott-bearing specimens. (Some of the *Paraconularia* terminate at a test width of up to about 5 mm, but this is still below levels of occurrence of terminal schotts in schott-bearing *Paraconularia* specimens here examined.) Most of the specimens (including all *Archaeoconularia granulata* and *Metaconularia manni*, and nearly all *Conularia trentonensis*) are flattened, having been preserved in shale or lime mudstone. For many of these specimens, the presence or absence of internal schotts had to be ascertained by checking for localized deformation of the faces (the test cavity of the remaining specimens has been revealed through exfoliation or sectioning). Two of the species chosen here, *Conularia splendida* and *C. trentonensis*, have yielded schott-bearing specimens. As shown in Text-figure 3, pointed *Conularia* specimens for which reliable estimates of original test length can be obtained fall within or close to the size range of schott-bearing, conspecific specimens whose original test length likewise can reliably be estimated.

None of the specimens in this sample exhibits internal schotts. A similar result was obtained by Barrande (1867), who found that schotts did not occur in the test cavity of several hundred Bohemian specimens, all belonging to genera that have yielded schott-bearing specimens but without a terminal schott themselves. Given that many of the specimens here examined are similar in size to conspecific specimens terminating in a schott (suggesting that the specimens were similar in age), these results tend to falsify the hypothesis that schott production was a regular feature of conulariid ontogeny.

DISTRIBUTION OF SCHOTT-BEARING SPECIMENS RELATIVE TO SEDIMENTARY FACIES

Background

As indicated by studies of the stratigraphy and sedimentology of strata known to bear conulariids (e.g. Branson 1944; Lowenstam 1957; Svoboda 1966; Belt *et al.* 1967; Scoffin 1971; Lane 1973;



TEXT-FIG. 3. A, Histogram showing the estimated original test lengths (as measured along the midlines) of 12 specimens of *Conularia splendida* Billings (Upper Ordovician, northeast Iowa, USA), including 9 pointed specimens (open bars; SUI 49979/3, 61511–61518) and 3 specimens terminating in a schott (solid bars; AC I-1448, SUI 61519–61520). B, Histogram showing the estimated original test lengths (as measured along the midlines) of 6 specimens of *C. trentonensis* Hall (Middle to Upper Ordovician, USA), including 3 pointed specimens (open bars; AMNH 29649, SUI 61506, UWGM WW4001) and 3 specimens terminating in a schott (solid bars; ROM 28324, SUI 61505, UMMP 66012). All of the specimens preserve (or come very close to preserving) their aperture. For all specimens, the position of the apex was estimated by extending the corners to their point of intersection.

Ramsbottom 1973; Bender 1974; Babin *et al.* 1976; Titus and Cameron 1976; Watkins 1978; Titus 1982, 1986; Shaver *et al.* 1986; Williams and Telford 1986; Harland and Pickerill 1982, 1987), conulariids occur in marine deposits spanning a more or less continuous spectrum of shallow nearshore to deep offshore facies. Based on levels of physical energy at the time of deposition, these facies can be interpreted as belonging to one of three general depositional regimes. Arranged in order of increasing energy, these are: (1) sheltered nearshore or deep, distal shelf or basinal waters that were characterized by extremely low physical energy; (2) moderately deep, mesial shelf waters, situated below fair-weather wave base but subject to episodes of relatively high current energy during storms; and (3) shallow, proximal shelf waters, situated closer to fair-weather wave base than Regime 2 settings and subject to more frequent and/or intense episodes of bottom turbulence.

Depositional Regime 1 is represented primarily by dark (grey to black), laminated shales, lime mudstones, and muddy siltstones, commonly with benthic macrofaunas that are sparse and of low diversity. As indicated by faunal and sedimentological evidence and by stratigraphic relationships (e.g. Belt *et al.* 1967; Lane 1973; Mikulic *et al.* 1985*a*, 1985*b*; Watkins 1978; Harland and Pickerill 1987), Regime 1 sediments were generally deposited in sheltered lagoons or embayments, or on the distal portions of marine shelves or in cratonic shale basins, below storm wave base.

Conulariids in at least some Regime 1 deposits (e.g. cementstones in the Calciferous Sandstone Group, Lower Carboniferous, Scotland; Belt *et al.* 1967) occur in probable life clusters. In these clusters, which consist of anywhere from 2 to 20 or more specimens, some or all of the specimens converge adapically on a common centre (e.g. Text-fig. 4A; see also discussions and illustrations in Slater (1907), Ruedemann (1925), Sinclair (1940), Lane (1973), and Babcock and Feldmann (1986*a*, 1986*b*)). In the remainder of this discussion, such clusters will be referred to as radial clusters.

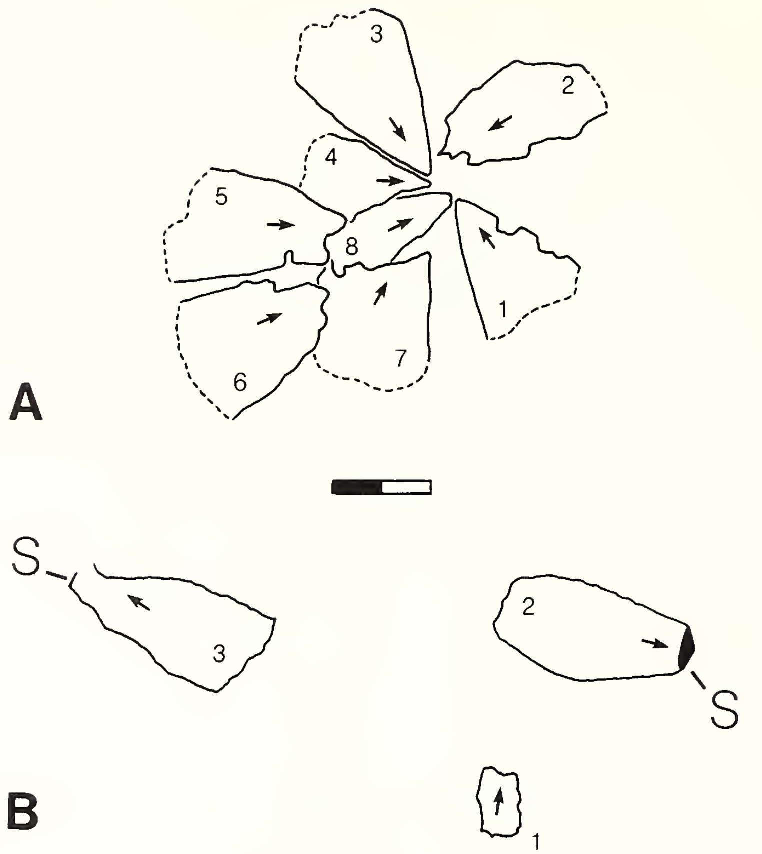
Depositional Regime 2 is represented primarily by light- to dark-coloured, mud-dominated shelf limestones (mudstones and wackestones), with minor amounts of bioclastic limestone, and by interbedded shales and fine sandstones. Faunas in these deposits are more diverse than faunas in Regime 1 deposits, with greater numbers of 'normal' shelf benthos such as articulate brachiopods, bryozoans, and echinoderms. Like conulariids in Regime 1 deposits, conulariids in Regime 2 deposits may be clustered; however, Regime 2 clusters almost never show a radial arrangement (indicating that they have been disrupted; see below). Although Regime 2 deposits contain substantial amounts of mud-sized sediment, suggesting deposition under conditions of low physical energy, episodes of relatively high energy are indicated by the presence of tempestite horizons (e.g. Titus 1982, 1986; Bakush and Carozzi 1986), characterized by sharp (scoured) lower contacts and, in the case of carbonates, packstone to grainstone fabrics (commonly with intraclasts and substantial fragmentation and abrasion of skeletal grains). Clastic analogues of Regime 2 carbonate deposits generally consist of alternating thin shales and fine- to medium-grained, argillaceous or micaceous sandstones (e.g. Havlíček and Vaněk 1966; Bender 1974).

Depositional Regime 3 is represented by thick, laterally extensive deposits of clean, fine- to coarse-grained quartz sandstone, and by carbonate deposits consisting mostly of mud-free, bioclastic limestone, with minor amounts of shale and/or muddy limestone. As indicated by sedimentological and stratigraphic evidence (e.g. Atherton *et al.* 1975; Johnson 1980), the bulk of these units was deposited under conditions of relatively high energy, probably associated with storms.

Clearly, the chances of live conulariids being subjected to current energy of sufficient magnitude to cause breakage would have been greater in Regime 2 or 3 environments than in Regime 1 environments. Thus, if schott formation was associated with repair of a severed apical end, one might expect to observe significantly greater proportions of schott-bearing specimens in Regime 2 and 3 samples than in samples from Regime 1. Since Regimes 2 and 3 were both characterized by episodes of relatively high physical energy (the distinction between these two regimes involving the frequency and intensity of such episodes), differences in the proportion of schott-bearing specimens between samples from Regimes 2 and 3 might not be significant.

Observations

Data on the frequency of occurrence of schott-bearing conulariid specimens in samples from the three depositional regimes outlined above are presented in Table 1. Schott-bearing specimens are extremely rare or absent (only 2 of 688 specimens examined) in samples from Regime 1 deposits, but they are common in samples from Regimes 2 (41 of 75 specimens examined) and 3 (162 of 810 specimens examined). Application of the chi-square statistic indicates that differences in the proportion of schott-bearing specimens between Regime 1 (2/668) and Regimes 2 (41/75) and 3 (162/810), respectively, are highly significant, with the chances that these differences are due to random sampling error being substantially less than 1 in 1000. Similar high confidence levels apply to comparisons involving conspecific specimens or congeneric specimens of very similar species only (see Table 1). (Due to factors associated with sample size, comparisons involving conspecific or



TEXT-FIG. 4. A, *Conularia splendida* Billings; SUI 49979; Upper Ordovician (Maquoketa Formation); northeast Iowa, USA; line drawing of a radial cluster consisting of eight specimens; the arrows indicate the directions in which the apical ends point; scale bar = 2 cm. B, *C. trentonensis* Hall; BMS E10807; Ordovician; New York, USA; line drawing of three specimens preserved on a slab of coarse, skeletal (brachiopod/bryozoan/echinoderm) lime grainstone; two of the specimens terminate in a schott (labelled 'S'). The three specimens are interpreted as members of a single, formerly radial cluster that underwent disruption and transport (see discussion in text).

congeneric specimens only are most appropriately evaluated using Fisher's Exact Test, discussed in detail by Bliss (1967).)

These results are reinforced by semi-quantitative observations on additional samples in the conulariid literature. Kowalski (1935, p. 291), discussing a sample of approximately 20 specimens of *Archaeoconularia pyramidata* (Hoeninghausen) from the Upper May ('*Conularia*') Sandstone (Upper Ordovician), northwest France, states that 'many specimens' terminate in a schott. Bouček (1928, p. 78), who examined approximately 200 specimens of *A. consobrina* (Barrande) from Middle Ordovician quartz sandstones in the Barrandian Basin, Bohemia, reports that 'the apex of the shell is almost always missing, and one finds in its place a hemispherical [schott].' Barrande (1867, p. 15), commenting on Barrandian Basin conulariids in general (a sample consisting of several thousand specimens), notes that 'in most species, especially those that [occur] in shales, we see conulariids terminating in a sharp point…[but] five of our species, preserved in quartzite…, show, in many cases, a [schott].' Similarly, Slater's (1907) data on the anatomy of British conulariids indicate that whereas conulariids from shallow-water, open shelf limestones (e.g. the Silurian Wenlock Limestone

Species	Unit and Age	Locality	Host Lithology	N	Ns	Np
Depositional Regime 1						
Archaeoconularia						
(1)*A. exquisita***	Middle Ordovician (1)	Bohemia	Dark shale	200	0	?(*)
Conularia						
(2)*C. trentonensis*	Collingwood Shale (U. Ordo., 2)	Ontario	Black, laminated shale	40	2	38
(2)*C. trentonensis*++	Tetreauville Fm. (M. Ordo., 3)	Quebec	Black, laminated lime mudstone	100	0	?(*)
(2)*C. trentonensis*	Brandon Bridge Fm. (Silur., 4)	Wisconsin	Grey, laminated shale	159	0	113
Metaconularia						
(3)*M. aspersa*	Lower Ludlow Shale (Silur., 5)	England	Grey-brown, laminated shale	3	0	2
(3)*M. bilineata***	Liten Fm. (Silur., 6)	Bohemia	Black, laminated calcareous shale	17	0	?
(3)*M. manni*	Lecthaylus Shale (Silur.)	Illinois	Grey, laminated shale	13	0	12
Paraconularia						
(4)*P. chagrinensis*	Chagrin Shale (U. Devon.)	Ohio	Grey, laminated shale	13	0	2
(4)*P. chesterensis**	Edwardsville Mbr., Muldraugh Fm. (Miss., 7)	Indiana	Grey, laminated shaley siltstone	53	0	?(*)
(4)*P. tenuis*+	Cementstone Facies, Calciferous Sandstone Gp. (Miss., 8)	Scotland	Grey, laminated lime mudstone	70	0	?(*)
Depositional Regime 2						
Conularia						
(5)*C. sowerbyii*	Wenlock Limestone (Silur., 9)	England	Lime mudstone/wackestone	25	14	0
(6)*C. subcarbonaria*	Keokuk Limestone (Miss., 10)	Illinois	Lime wackestone/packstone/grainstone	10	5	0
(6)*C. subcarbonaria*	Ramp Creek Mbr., Harrodsburg Limestone (Miss., 11)	Indiana	Lime wackestone/packstone	1	0	0
(7)*C. trentonensis*	Verulam Fm. (M. Ordo., 2)	Ontario	Lime wackestone/packstone/grainstone	11	5	0
(7)*C. trentonensis*	Denley, Kings Falls, Sugar River Fms. (M. Ordo., 12)	New York	Lime wackestone/packstone/grainstone	11	6	0
(7)*C. trentonensis*	Sherwood Mbr., Dunleith Fm. (M. Ordo., 13)	Iowa	Lime wackestone/packstone	8	2	0
Metaconularia						
(8)*M. calderi*	Verulam (Cobourg) Fm. (M. Ordo., 2)	Ontario	Lime wackestone/packstone/grainstone	3	3	0
(8)*M. divisa*	Dubuque Fm. (U. Ordo., 13)	Iowa	Lime mudstone/wackestone	5	5	0
(8)*M.* sp.	Lower Lindsay Fm. (M. Ordo., 14)	Ontario	Lime wackestone/packstone	1	1	0
Depositional Regime 3						
Anaconularia						
(9)*A. anomala*	Drabov Quartzite (M. Ordo., 1)	Bohemia	Fine to medium, micaceous quartz sandstone	760	140	0
Archaeoconularia						
(10)*A. consobrina*	Drabov Quartzite (M. Ordo., 1)	Bohemia	Fine to medium, micaceous quartz sandstone	10	5	0
(10)*A. pyramidata*	Upper May (*Conularia*) Sandstone (U. Ordo., 15)	Brittany	Fine to coarse quartz sandstone	20	10	0
Conularia						
(11)*C. subcarbonaria*	Burlington Limestone (Miss., 16)	Missouri	Coarse, skeletal lime grainstone	11	3	0
(12)*C. trentonensis*	Ordovician	New York	Coarse, skeletal lime grainstone	3	2	0
Paraconularia						
(13)*P.* sp.	Burlington Limestone (Miss., 10)	Iowa	Coarse, skeletal lime grainstone	5	2	0
(13)*P.* sp.	Glen Dean Limestone (Miss., 11)	Indiana	Coarse, skeletal lime grainstone	1	0	0

TABLE 1. Frequency of occurrence of schott-bearing conulariid specimens in samples from the three depositional regimes outlined in the text. Lettered symbols are as follows: N = number of specimens; Ns = number of specimens terminating in a schott; Np = number of pointed specimens (specimens tapering to a width of 1 mm or less and lacking a terminal schott). Sources of numerical data taken from the literature are as follows: ** = Bouček (1928); ++ = Sinclair (1948); * = Lane (1973); + = Slater (1907). An asterisk following a question mark in the Np column indicates that the percentage of pointed specimens is reported to be large. Numbers following the geologic age of the host rock unit refer to one of the following sedimentological and/or stratigraphic studies: 1, Havlíček and Vaněk (1966); 2, Brett and Brookfield (1984); 3, Harland and Pickerill (1982); 4, Mikulic *et al.* (1985*a*, 1985*b*); 5, Watkins (1978); 6, Svoboda (1966); 7, Lane (1973); 8, Belt *et al.* (1967); 9, Scoffin (1971); 10, Atherton *et al.* (1975); 11, Shaver *et al.* (1986); 12, Titus (1982, 1986) or Titus and Cameron (1976); 13, Bakush and Carozzi (1986); 14, Williams and Telford (1986); 15, Babin *et al.* (1976); 16, Branson (1944). See Appendix 3 for information on specimen locations. Numbers in parentheses preceding species names designate samples used in statistical analysis. Conspecific specimens from different localities but similar deposits were combined into one sample. In some cases, congeneric specimens from the same depositional setting were also combined to form a single sample (to compensate for small numbers of specimens and/or restriction of species to a single depositional setting). Statistical analysis was conducted on the following sample pairs: 1–4 vs 5–8; 1–4 vs 9–13; 1 vs 10; 2 vs 5; 2 vs 6; 2 vs 7; 2 vs 11; 2 vs 12; 3 vs 8; 4 vs 13.

(Scoffin 1971) and the Carboniferous Limestone (Ramsbottom 1973)) often terminate in a schott, conulariids from dark, graptolitic slates and shales, deposited in settings further offshore (Rayner 1967), do not exhibit a schott but commonly taper to a point.

Discussion

The foregoing results falsify the hypothesis that schott-bearing conulariids were similar to scyphozoan medusa, but they are consistent with the hypothesis that schott-bearing conulariids represent living individuals severed by currents. Additional lines of evidence suggest that patterns of occurrence observed here are not the result of other causes, for example mass mortality of very young conulariids (killed before they had the chance to form schotts), or inhibition of schott formation by other factors of the local environment (e.g. low dissolved oxygen content). Although many of the conulariids examined here have been broken well below the aperture (making it impossible to obtain reliable measurements of the original size of these specimens), those Regime 1 specimens that are more or less intact are generally similar in size to conspecific or congeneric, schott-bearing specimens from Regime 2 and 3 deposits, and thus it seems unlikely that low frequency of occurrence of schott-bearing specimens in Regime 1 samples is due to unusually early death. This conclusion is reinforced by data in Barrande (1867) indicating that Bohemian *Archaeoconularia* (Table 1) from dark shales (Regime 1) are about as large as morphologically similar, schott-bearing *Archaeoconularia* collected from quartz sandstones (Regimes 2 and 3). Together with the observation that Regime 1 specimens here examined show no other evidence of abnormal development (e.g. departure from patterns of test ornamentation exhibited by specimens from Regime 2 or 3 deposits), these observations also tend to rule out the hypothesis that low frequency of occurrence of schott-bearing specimens in Regime 1 deposits is due to inhibition of schott formation by unfavourable environmental conditions.

Data obtained at finer scales of observation lend additional support to the hypothesis that schott formation was prompted by severance. For example, the one Regime 1 sample here encountered that contains schott-bearing specimens (*Conularia trentonensis* Hall, Collingwood Shale; 2 schott-bearing specimens out of 40 specimens sampled) appears to differ from several other Regime 1 deposits in lacking radial clusters. This suggests that Collingwood conulariids were subjected to some degree of disturbance, possibly associated with storm events affecting adjacent, shallower-water shelf environments (Brett and Brookfield 1984).

Evidence of disturbance is exhibited by many of the conulariids from Regimes 2 and 3. Conulariid steinkerns consisting of quartz sandstone often contain large amounts of medium to coarse sand (see also Kowalski 1935), suggesting that the horizons that yielded these specimens were deposited under conditions of relatively high energy. Similarly, most of the schott-bearing specimens from Regime 2 carbonates occur in a wackestone or packstone matrix rich in disarticulated echinoderm ossicles and disarticulated and/or broken trilobites and brachiopods, suggesting that they were collected from tempestite horizons. At least five of the schott-bearing specimens examined here occur in non-radial clusters (e.g. Text-fig. 4B). The three-specimen cluster shown in Text-figure 4B, which includes two specimens terminating in a schott, occurs in coarse, bioclastic limestone. Conulariids in the units from which this and similar clusters were collected are so rare (Van Iten in prep.) that it seems extremely unlikely that they are artefacts of concentration by currents or scavengers. Rather, they seem best interpreted as former life clusters. Coupled with sedimentological evidence indicating current action, the present non-radial arrangement of specimens in these clusters suggests that they were physically disrupted. As expected, schott-bearing specimens do not occur in currently known radial clusters (Van Iten in prep.), which have undergone little or no disruption.

CONCLUSION

Analyses of the anatomy and patterns of occurrence of the conulariid schott show that schotts do not occur in the test cavity of specimens that lack a terminal schott and are preserved close to the apex, and that schott-bearing conulariids occur in significantly higher proportions in samples from high-energy deposits than in samples from low-energy deposits. These results corroborate the hypothesis that schott-bearing conulariids represent living individuals severed by currents, but they are inconsistent with other previously suggested interpretations of schott-bearing conulariids. The occurrence of specimens having more than one schott, interpreted by some investigators (e.g. Hall 1847) as evidence that schott formation was a regular feature of conulariid ontogeny, is not necessarily inconsistent with the hypothesis that schott-bearing conulariids were severed in life. As an example, severed individuals may have been susceptible to infection or necrosis, leading to additional episodes of schott formation.

Certainly, previously offered interpretations of schott-bearing conulariids do not exhaust the full array of interpretations that might reasonably be suggested by analogy with living organisms. However, none of these interpretations (e.g. obligatory decollation of the apical end, encystment) appears to carry with it the expectation that schott-bearing conulariids should occur in significantly higher proportions in high-energy deposits than in low-energy deposits.

Although schott-bearing specimens probably were not medusa-like, as held by Kiderlen (1937) and several other proponents of a scyphozoan affinity for conulariids, this does not necessarily mean that conulariids did not produce medusae (through means other than direct transformation of test-bearing, polypoid individuals; e.g. Van Iten 1989, 1991*b*). Moreover, even if conulariids did not produce medusae, this alone would not mean that conulariids and scyphozoans were not closely related to each other, since some scyphozoans lack a medusa (Hyman 1940).

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HEYO VAN ITEN

Museum of Paleontology
University of Michigan
Ann Arbor, MI 48109, USA

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APPENDICES

The following three appendices list conulariid specimens used as data in the present study. Abbreviations of repositories housing these specimens are as follows: AC, Augustana College, Rock Island, Illinois; AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), London; BM-UW, Burke Museum, University of Washington, Seattle; BMS, Buffalo Museum of Science, Buffalo; BUGM, Birmingham University Geology Museum, Birmingham; CM, Carnegie Museum of Natural History, Pittsburgh; CMNH, Cleveland Museum of Natural History, Cleveland; FMNH, Field Museum of Natural History, Chicago; GSC, Geological Survey of Canada, Ottawa; ISGS/ISM, Illinois State Geological Survey/Illinois State Museum, Champaign/Urbana; IUPC, Indiana University, Paleontological Collections, Bloomington; NYSM, New York State Museum and Science Service, Albany; SUI, State University of Iowa, Iowa City; UMMP, University of Michigan Museum of Paleontology, Ann Arbor; UMMP*, University of Montana Museum of Paleontology, Missoula; USNM, United States National Museum, Washington; UWGM, University of Wisconsin Geological Museum, Madison.

APPENDIX 1

List of conulariid specimens terminating in a schott and examined for the presence of schotts within the test cavity. Species followed by an asterisk are preserved as sandstone steinkerns. N = number of specimens examined.

Species	Repository	N
*Anaconularia anomala** (Barrande)	MCZ	144
*Archaeoconularia consobrina** (Barrande)	MCZ	5
A. dubia (Sinclair)	ROM 18889	1
*A. pyramidata** (Hoeninghausen)	FMNH PE294, PE379-382; GSC 87183; ROM 22289, 22532	9
Conularia multicostata Meek and Worthen	AC I4160, I4164	2
C. quichua Ulrich	USNM 373992	1
C. sp.	UMMP 259	1
C. sp.	ISGS/ISM 4434	1
C. sp.	SUI 62675*a*	1
C. splendida Billings	SUI 61519-61520	2
C. subcarbonaria Meek and Worthen	FMNH UC18494, UC19647; ISGS/ISM 2609; MCZ 27951, 27954–27955	7
C. trentonensis Hall	AMNH 29650, 42316; BMS 10804; NYSM 3492; ROM 67, 23278, 23737, 23738, 24007, 28324, 24917; SUI 61502; UMMP 66012–66016; UMPC W1991	25
Metaconularia calderi Sinclair	GSC 9794–9795	2
M. sp.	ROM 87DR	1
M. divisi Sinclair	SUI 53089, 62678–62679	3
Paraconularia byblis (White)	UMMP 2167	2

APPENDIX 2

List of conulariid specimens not terminating in a schott and examined for the presence of schotts within the test cavity. The letter P following a specimen number or numbers indicates that the corresponding specimen or specimens taper to a test width of 1 mm or less.

Species	Repository
Archaeoconularia granulata (Hall)	AMNH 791(P) (2 specimens)
Conularia splendida Billings	SUI 499793(P) (1 specimen), SUI 61511–61518(P) (8 specimens)
C. trentonensis Hall	AMNH 29649(P) (1 specimen); SUI 61506 (1 specimen); UWGM WW4001(P) (113 specimens)
Metaconularia manni (Roy)	FMNH PE6252–6256(P), PE10132(P), PE23674–23675(P), unnumbered(P) (12 specimens)
Paraconularia chagrinensis Babcock and Feldmann	CMNH 1788(P), 6633 (3 specimens)
P. chesterensis (Worthen)	GSC 49383 (1 specimen)
P. recurvatus Babcock and Feldmann	USNM 409806 (1 specimen)
P. subulata (Hall)	CM 34521, 34524 (2 specimens); CMNH 1788, 6633 (3 specimens); UMMP* 5613A/I7106, 5628NC/MI7106 (2 specimens)
P. yochelsoni Babcock and Feldmann	UMMP 45499(P), 45500(P) (3 specimens)

APPENDIX 3

Specimen numbers for samples listed in Table 1.

Species	Repository
Depositional Regime 1	
Conularia	
C. trentonensis Hall (Collingwood Fm.)	ROM 27274 (40 specimens)
C. trentonensis Hall (Brandon Bridge Fm.)	UWGM WW4001 (159 specimens)
Metaconularia	
M. aspersa (Slater)	BMNH G4603, G5373, G12879 (3 specimens)
M. manni (Roy)	FMNH PE6252–6256, PE10132, PE23674–23975, FMNH unnumbered (13 specimens)
Paraconularia	
P. chagrinensis Babcock and Feldman	CMNH 1247, 1272, 1427, 1622, 1674, 1788, 1818, 4030, 4292, 6633, 6717, 6807–6808 (13 specimens)
Depositional Regime 2	
Conularia	
C. sowerbyii (Slater)	BMNH 6275, 6327, 10043, 11795, 17500–17505, unnumbered (14 specimens); UBGM 'Holcroft Pteropoda' (10 specimens)
C. subcarbonaria (Meek and Worthen)	FMNH UC18494, UC19647, FMNH unnumbered (8 specimens); ISGS/ISM 2609 (1 specimen); ISM 2609 (1 specimen); IUPC 17482 (1 specimen)
C. trentonensis Hall (Verulam Fm.)	ROM 67, 23738 (512T), 24917 (24OU) (9 specimens); GSC 1725–1726 (2 specimens)
C. trentonensis Hall (Denley Fm.)	UMMP 66012–66022 (11 specimens)
C. trentonensis Hall (Sherwood Mbr.)	SUI 61502–61505 (8 specimens)
Metaconularia	
M. calderi Sinclair	GSC 9794–9795 (2 specimens); Sinclair (1940, pl. 3, figs 3–5; 1 specimen)
M. divisa Sinclair	BM-UW (2 specimens); SUI 53089, 62678–62679 (3 specimens); UMPC W1994 (3 specimens); Sinclair (1948, pl. 8, figs 12–14; 1 specimen)
M. sp.	ROM 87DR (1 specimen)
Depositional Regime 3	
Anaconularia	
A. anomala (Barrande)	MCZ (760 specimens)
Archaeoconularia	
A. consobrina (Barrande)	MCZ (10 specimens)
A. pyramidata (Hoeninghausen)	BMNH 3408–3409 (9 specimens); FMNH PE294, PE379–382, FMNH unnumbered (7 specimens); GSC 87180 (1 specimen); ROM 22289, 22532 (3 specimens)
Conularia	
C. subcarbonaria Meek and Worthen	MCZ 27946–27956 (11 specimens)
C. trentonensis Hall	BMS E10807 (3 specimens)
Paraconularia	
P. sp.	USNM 57164, 99502 (4 specimens); ISGS (ISM) 10742 (4291) (1 specimen); IUPC 6071 (1 specimen)